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Macrofaunal distributions and habitat change following winter–spring releases of freshwater into the Breton Sound estuary, Louisiana (USA)

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Abstract

We examined the effect of freshwater inflows on the aquatic environment and macrofauna in the intermediate and brackish zones of the Breton Sound estuary. Following water releases from the Caernarvon Freshwater Diversion Structure in winter 2000 and spring 2001, we compared environmental conditions and the abundance and distribution of nekton in May 2001 between the inflow area, which receives freshwater directly from the structure, and a nearby reference area. We used these data and stable isotope analyses for C, N, and S in brown shrimp *Farfantepenaeus aztecus* and two species of grass shrimp (*Palaemonetes paludosus* and *Palaemonetes intermedius*) to test four null hypotheses: (1) water quality and SAV (submerged aquatic vegetation) coverage were similar between the inflow and reference areas, (2) macrofaunal abundance and biomass were similar between the two areas, (3) stable isotopic values of brown shrimp and grass shrimp were similar between areas, habitat types, and species, and (4) brown shrimp distributions were unaffected by river inputs. Freshwater from the structure clearly influenced the estuarine environment within the inflow area. Releases from the Caernarvon structure freshened the inflow area as intended and increased SAV and daytime dissolved oxygen concentrations. The response by macrofauna to these increased freshwater flows and habitat changes involved mostly changes in density and biomass rather than shifts in species composition. Although we detected no strong effect of the freshwater diversion on brown shrimp abundance or size in the inflow area, results of the sulfur stable isotope analysis indicated that brown shrimp collected in the inflow area had been growing in higher salinity waters, possibly following downstream displacement by the diversion. Species that would benefit most from continued freshwater diversions are likely to be those species that both use SAV as nursery habitat and thrive in a low-salinity environment. Nutrients carried by water from the structure were incorporated into the estuarine food web, and these nutrient inputs, together with an increase in SAV habitat, may enhance overall secondary productivity in the inflow area.

Keywords: river diversion; brown shrimp; *Farfantepenaeus aztecus*; salinity; restoration; SAV; submerged aquatic vegetation

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1. Introduction

Siphons and water-control structures of various sizes are currently being used in Louisiana to divert water from the Mississippi River into nearby estuaries. The management goals of these freshwater diversions are to control salinity, improve water quality, restore coastal wetlands, increase fishery production, and reduce the threat of flooding to downstream urban areas. Many additional large capacity structures are also being planned in the state to divert Mississippi River water into coastal areas for wetland restoration.

Increased inflow of freshwater influences numerous estuarine characteristics that affect primary and secondary productivity (Alber, 2002). For example, freshwater inflows directly alter estuarine salinities, which can influence the distribution and productivity of estuarine animals. Estuarine salinities respond to the volume and timing of freshwater inflows, and these factors have been related to the productivity of important coastal fisheries (Gunter and Hildebrand, 1954; White and Perret, 1974; Browder, 1985; Flint, 1985; Gracia, 1991; Gammelsrød, 1992; Wilber, 1994; Loneragan and Bunn, 1999; Galindo-Bect et al., 2000).

Freshwater releases from the Caernarvon Diversion Structure located in southeast Louisiana are controlled to avoid potential negative impacts to brown shrimp *Farfantepenaeus aztecus* (Ives) in the Breton Sound estuary. High flows that would substantially alter salinity in the estuary are not released from the structure in April and May when brown shrimp are most abundant in estuarine nursery areas.

The evidence from the scientific literature for a salinity effect on brown shrimp recruitment, distribution, growth, and production, however, is not clear. In a laboratory setting at temperatures of 24.5–26.0 °C, brown shrimp postlarvae survived and grew equally well in salinities[1] of 2–40 (Zein-Eldin, 1963). Survival of postlarvae decreased in salinities <5, however, when temperatures were <15 °C (Zein-Eldin and Aldrich, 1965). Saoud and Davis (2003) reported juvenile brown shrimp growth to be significantly higher at salinities of 8 and 12 than at 2 and 4. In a laboratory salinity gradient (0–70), Keiser and Aldrich (1973) found that postlarval brown shrimp selected for salinities mainly between 5 and 20. Numerous studies based on field observations have reported an effect of salinity on the abundance and distribution of brown shrimp. The conclusions of these studies, however, have not been consistent and range from reports that brown shrimp were most abundant at salinities >15 (e.g., Longley, 1994) to those showing that most shrimp occurred at salinities <5 (e.g., Parker, 1970). It is difficult to assess the effect of salinity or freshwater flow on shrimp populations because many variables other than salinity can influence recruitment and may confound the results of most field studies.

Freshwater inflows not only dilute salinity, but also carry distinct stable isotope values that can be traced through the estuarine food web. Stable isotope analysis, therefore, provides a powerful tool for examining the connection between freshwater inflows from river diversions and estuarine consumers (Fry, 2002a).

The objective of our study was to document springtime habitat conditions and distribution patterns of brown shrimp and other species of nekton in the vicinity of the Caernarvon Diversion Structure. Densities of nekton and environmental variables within intermediate and brackish marsh zones were documented and compared between an area that receives freshwater directly from the structure (henceforth referred to as the inflow area) and a nearby reference area to assess the effect of freshwater flows from the structure on habitat use. In addition, we used stable isotope analyses of brown shrimp and grass shrimp tissues to examine the effect of the diversion on these estuarine consumers. These density and stable isotope data were used to test four null hypotheses: (1) water quality and SAV (submerged aquatic vegetation) coverage were similar between the inflow and reference areas, (2) macrofaunal abundance and biomass were similar between the two areas, (3) stable isotopic ^{13}C, ^{15}N, and ^{34}S compositions of brown shrimp and grass shrimp were similar between areas, habitat types, and species, and (4) brown shrimp distributions were unrelated to river inputs from the diversion.

2. Study areas

The Breton Sound estuary is located in southeastern Louisiana, and is bounded on the north by the Mississippi River Gulf Outlet and on the south by the Mississippi River (Fig. 1). The Caernarvon Freshwater Diversion Structure was constructed in 1991 at the head of the estuary near Big Mar and is capable of diverting 226 $m^3 s^{-1}$ (8000 $ft^3 s^{-1}$) of Mississippi River water into the Breton Sound Basin (USACOE, 1993; Lane et al., 1999). The structure has been operated since its construction to reduce oyster mortality from predation by lowering salinities at the productive oyster seed grounds in the basin. A second goal of the diversion is to halt the conversion of fresh and intermediate marshes (i.e., prime alligator, muskrat, and waterfowl habitat) to brackish and saline marshes. Most of the freshwater released by the Caernarvon structure flows south and east, and little, if any, of this flow is thought to reach that portion of the basin north of Bayou Terre Aux Boeufs (Fig. 1). Because freshwater inflows from the

[1] The Practical Salinity Scale was used for measuring and reporting all salinity values.

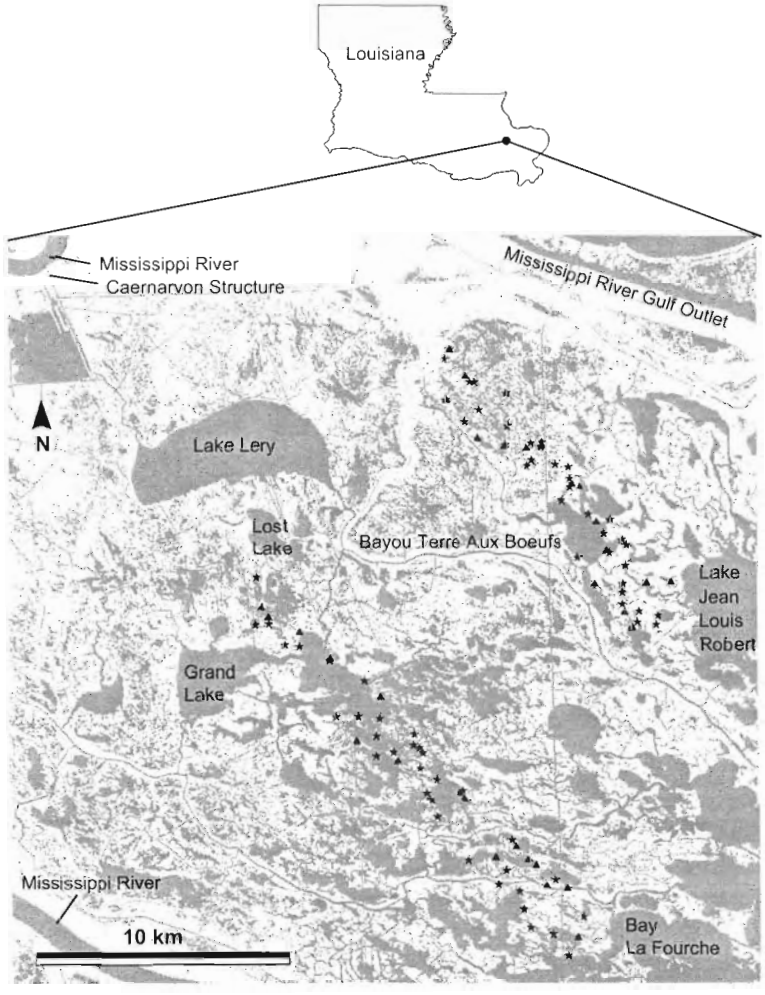

Fig. 1. Map of the study area showing the two transects and 100 sample sites within the Breton Sound estuary. The inflow and reference areas are located south and north, respectively of Bayou Terre Aux Boeufs. Marsh sample sites are shown as triangles. Water (SAV, submerged aquatic vegetation, and SNB, subtidal nonvegetated bottom) sample sites are represented by stars. The location of the Caernarvon Diversion Structure is shown northwest of Lake Lery.

structure should only effect macrofaunal populations south of Bayou Terre Aux Boeufs, we selected the area north of Bayou Terre Aux Boeufs as a reference area for our study.

3. Methods

3.1. Nekton samples

We sampled marsh and pond areas along two transects within the intermediate and brackish marsh zones of the Breton Sound Basin May 7–11, 2001 (Fig. 1). Our sampling effort followed prolonged releases of freshwater from the Caernarvon structure during winter 2000 and spring 2001 (Lane et al., 2004). All samples were taken at randomly-selected sites along two northwest–southeast oriented transects between Lost Lake and Bay La Fourche in the inflow area and from Louisiana Highway 300 to Lake Jean Louis Robin in the reference area. We located sites along these two approximately 2-km wide by 20-km (inflow area) and 14-km (reference area) long transects to ensure that our sample sites were spread across the intermediate and brackish marsh zones of both areas.

We collected 16 samples on the marsh surface and 34 samples in open water in each area (inflow and reference) using a 1 m^2 drop sampler (Zimmerman et al., 1984) for a total of 100 samples. We chose a drop sampler for this study because it is effective in dense emergent vegetation, and the catch efficiency of this enclosure device does not appear to vary substantially with habitat characteristics typical of shallow estuarine areas (Rozas and Minello, 1997). The sampler was a 1.14-m-diameter cylinder that we dropped from a boom attached to a shallow-draft boat. The boat (unpowered) was allowed to drift until the cylinder was over a sample site or two persons positioned the cylinder over a sample site by slowly

pushing from the boat's stern. When released from the boom, the cylinder rapidly entrapped organisms within a 1.0-m^2 sample area. We collected more samples in open water (submerged aquatic vegetation = SAV or subtidal nonvegetated bottom = SNB) than on the marsh surface to ensure that at least some of these sites contained SAV.

After the cylinder was dropped, we measured water temperature, dissolved oxygen, salinity, and turbidity using the methods described by Minello and Zimmerman (1992). We determined water depth at each sample site by averaging five depth measurements taken within the sampler. We also measured the distance from the middle of the sample area to the nearest marsh–water interface. At marsh sites, plant stems were clipped at ground level, counted (dead and alive combined), and removed from the cylinder. If SAV was present at open-water sites, we estimated coverage within the sampler (0–100%) and identified the species of plants present.

After measuring the environmental variables, we captured nekton trapped in the drop sampler by using dip nets and filtering the water pumped out of the enclosure through a 1-mm-mesh net. When the sampler was completely drained, any animals remaining on the bottom were removed by hand. Samples were preserved in 10% formalin and returned to the laboratory for processing.

In the laboratory, the samples were sorted, and animals were identified to lowest feasible taxon. We used the nomenclature of Perez-Farfante and Kensley (1997) for penaeid shrimps and identified species using the protocol described in Rozas and Minello (1998). Twenty specimens of *Farfantepenaeus* could not be reliably identified either because of their size (total length 13–18 mm) or because they were damaged; these shrimps were assigned as brown shrimp *Farfantepenaeus aztecus* (Ives) or pink shrimp *Farfantepenaeus duorarum* (Burkenroad) based on the proportion of identified species in each sample. Animals that could not be reliably identified were not used in size analyses. Total length (TL) of fishes and shrimps and carapace width (CW) of crabs were measured to the nearest mm. We determined the biomass for each species by pooling individuals in a sample and measuring wet weight to the nearest 0.1 g.

3.2. Isotope analysis

A total of 37 brown shrimp (inflow area = 17; reference area = 20) and 39 grass shrimp (*Palaemonetes paludosus*: inflow area = 20, reference area = 1; *Palaemonetes intermedius*: inflow area = 9, reference area = 9) samples were used for stable isotope analysis. These samples consisted of pooled shrimp (1–5 individuals) collected at the same site and time. To reduce the variability of isotopic values associated with different tissue types (Schmidt et al., 2004), we only used muscle tissue that was dissected from the tail of each specimen. This dissected tissue was rinsed, dried at 60 °C, pulverized, and analyzed for elemental and isotopic compositions with an integrated system consisting of an elementary analyzer linked to an isotope ratio mass spectrometer (Barrie and Prosser, 1996; Monaghan et al., 1999; Fry et al., 2002). Results are reported in δ notation relative to international standards PeeDee *Belemnitella americana* (PDB) for $\delta^{13}C$, N_2 in air for $\delta^{15}N$, and Canyon Diablo Troilite (CDT) for $\delta^{34}S$. Isotopic abundances are given as:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right]1000$$

where X is ^{15}N, ^{13}C or ^{34}S, and R is $^{15}N/^{14}N$, $^{13}C/^{12}C$ or $^{34}S/^{32}S$.

Samples split in the laboratory and analyzed in duplicate usually gave isotopic compositions that agreed within a 0.5‰ range.

4. Statistical analyses

We used a one-way Analysis of Variance (ANOVA) followed by a priori contrasts to examine differences in densities and biomass of brown shrimp and other selected taxa, sizes of selected species, and environmental characteristics (salinity, water temperature, dissolved oxygen, water depth, turbidity, and distance-to-edge) among habitat types (inflow marsh, reference marsh, inflow SAV, reference SAV, and reference SNB). We examined inflow impacts and effects of habitat types using a priori contrasts. The first two contrasts compared marsh and SAV habitat types between the inflow and reference areas. The third contrast was designed to compare open-water sites between the inflow and reference areas. We used the fourth contrast to test for differences between marsh and SAV habitat types. Regression models and Analysis of Covariance (ANCOVA) were used to examine potential relationships between salinity and brown shrimp density in the basin. We considered alpha levels of 0.05 to be significant in all results, but we also assessed significance after adjusting alpha levels for the Habitat Type effect using the sequential Bonferroni method described by Rice (1989), which buffers against error introduced by making multiple comparisons with the same sample set (i.e., testing a hypothesis for several species or variables). Densities and biomass of animals were positively related to the standard deviation; therefore, we performed a $\ln(x + 1)$ transformation of the original values prior to analyses. Other variables were not transformed. In addition to simple regressions between salinity and nekton abundance in samples to look for relationships, we also classified samples into whole-number salinity classes (i.e., 1, 2, 3...n) and regressed salinity class with mean nekton abundance. This analysis removes variability in the dependent variable (abundance).

All tabular and graphical data presented in this paper are untransformed means. We conducted these statistical analyses using SuperANOVA (Version 5 Ed., Abacus Concepts, Inc., Berkeley, California, 1989) and Statview (Version 4.5 Ed., Abacus Concepts, Inc., Berkeley, California, 1995).

To investigate potential associations between taxa and environmental variables, we performed canonical correspondence analysis (CCA, CANOCO version 4). CCA is a direct gradient analysis that relates the pattern of community variation to the pattern of environmental variables (Ter Braak and Prentice, 1988). Compared to other ordination techniques, CCA has several advantages; it is fairly robust and unaffected by data transformations (Jackson, 1993, 1997), and it performs well for nonlinear and unimodal relationships between species and environmental variables, which usually cause severe problems for linear ordination methods such as principal components analysis (Ter Braak, 1986). We included all environmental variables in the CCA that had been previously analyzed in our ANOVA models, namely area, habitat, salinity, oxygen, water temperature, turbidity, stem density, distance-to-edge, water depth, and SAV coverage. Only marsh and open water were used as habitat types because SAV coverage of 0% perfectly described SNB and made this habitat class redundant. Fish and crustacean abundances were log-transformed. We performed 1000 Monte Carlo simulations to evaluate the significance levels of these variables for CCA. Significance of the CCA axes was evaluated by running 1000 unrestricted Monte Carlo simulations using the eigenvalues of the axes as test statistics. Initially, we used the whole data set including all 100 stations, and subsequently, we performed CCA on the inflow and reference areas alone.

To assess the effects of location, habitat, and species, we performed three-way ANOVAs for C, N, and S isotopic values (SAS version 9.0, SAS Institute Inc., Cary, NC, USA, 2002). Since we could not detect any significant differences between SAV and SNB sites, or the two species of grass shrimp, the final analyses resulted in a $2 \times 2 \times 2$ factorial design, testing the effects of location (inflow vs reference areas), habitat (marsh vs open water), and species (brown shrimp vs grass shrimp) on isotopic signatures. To account for the unequal sample sizes, we used the Satterthwaite method to estimate the degrees of freedom for the fixed effects, and the p-values of pair wise comparisons were adjusted using the Tukey method.

5. Results

5.1. Habitat characteristics

We found measurable differences in environmental conditions between the inflow and reference areas (Table 1). Although salinities along both transects increased with distance down the estuary (Fig. 2), freshwater flows from the structure reduced average salinities in the inflow area by approximately 3 (from 8.6 to 5.9) relative to the reference area. These inflows and lower salinities coincided with increased growth of SAV in the inflow area. All 34 open-water sample sites in the inflow area contained submerged vegetation (either rooted vascular plants or macroalgae), whereas only 20 of 34 open-water sample sites in the reference area contained these aquatic plants (100% vs 59%). Because samples were randomly allocated within the water depths we could sample, these data provide an estimate of SAV coverage in shallow (≤ 1 m) water. The areal coverage of SAV (rooted vascular plants only) was significantly greater in the inflow area than the reference area (66% vs 18%). Most SAV sites contained *Myriophyllum spicatum* and *Potamogeton pusillus*. *Ruppia maritima*, *Najas guadalupensis*, and *Ceratophyllum demersum* also were common, but less abundant. Daytime dissolved oxygen levels also were measurably higher in the inflow area (Table 1), presumably because of the prevalence of SAV in this area.

Macroalgae (an unidentified green alga and a *Nitella* spp.) also were widespread in the study area. Sixteen inflow sites and 12 reference sites contained macroalgae, and macroalgae coverage was 100% at three inflow sites and one reference site. Three inflow sites and nine reference sites contained only macroalgae and no SAV. We placed these 12 open-water sites in the "SAV habitat type" category, because macroalgae at these sites provided vegetation structure similar to other aquatic plants.

We also found detectable differences in environmental variables among habitat types. Marsh sites generally had higher turbidity levels, higher water temperature, higher salinity, and lower water depth than SAV sites, and (as expected) SAV sites were farther from the shoreline than marsh sites (Table 1). All marsh sites were within 2 m of the shoreline (Table 1). Marsh in the inflow area was flooded more deeply and had lower turbidity levels than marsh sites in the reference area (Table 1).

5.2. Nekton

We collected a total of 4596 animals (23 fish species and 10 decapod crustacean species) with a biomass of 1.94 kg wet weight in 100 samples (Tables 2 and 3). Fishes accounted for 65% of the organisms, whereas decapod crustaceans composed 84% of the biomass in our samples. Most decapod crustaceans (96.0%) and fishes (88.7%) were <50 mm in size. Therefore, our samples contained all life stages of small resident species, but nearly all fishery species were small juveniles.

Table 1
Environmental characteristics of habitat types within inflow and reference areas. Mean and (1 S.E.) are given for variables measured in marsh vegetation (marsh edge), in submerged aquatic vegetation (SAV), and over nonvegetated bottom (SNB) within the inflow and reference areas sampled in May 2001. Each mean is estimated from *n* samples shown in parentheses below each habitat type (except stems: 15 samples in each marsh). Results (*p* values) are given for ANOVA analyses we used to compare means among habitat types (except for stem density and SAV coverage where comparisons are between inflow and reference areas) and a priori contrasts testing for significant differences between: 1 = marsh in the inflow area and marsh in the reference area, 2 = SAV in the inflow area and SAV in the reference area, 3 = SAV in the inflow area and SAV + SNB in the reference area, and 4 = marsh in the two areas and SAV in the two areas. An asterisk (*) indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989). We used data for rooted vascular plants only to calculate SAV coverage for this table

Species	Inflow area		Reference area			ANOVA	Contrast *p* values			
	Marsh edge ($n = 16$)	SAV ($n = 34$)	Marsh edge ($n = 16$)	SAV ($n = 20$)	SNB ($n = 14$)	Habitat effect	(1) I Marsh vs R Marsh	(2) I SAV vs R SAV	(3) I SAV vs R SAV + R SNB	(4) I Marsh + R Marsh vs I SAV + R SAV
	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	*p* value				
Salinity (‰)	7.8 (0.68)	5.9 (0.37)	8.6 (0.52)	8.6 (0.48)	8.7 (0.51)	0.0001*	0.3039	0.0001	0.0001	0.0489
Oxygen (ppm)	8.3 (0.67)	7.8 (0.35)	4.9 (0.37)	5.9 (0.32)	4.8 (0.39)	0.0001*	0.0001	0.0007	0.0001	0.5511
Water temperature (°C)	28.1 (0.38)	26.9 (0.22)	27.2 (0.33)	27.1 (0.27)	25.9 (0.33)	0.0010*	0.0555	0.6556	0.2013	0.0424
Water depth (cm)	18.3 (2.17)	71.8 (1.55)	11.8 (1.35)	69.2 (1.94)	68.2 (3.64)	0.0001*	0.0493	0.3066	0.1671	0.0001
Turbidity (FTU)	11.8 (5.60)	3.0 (0.65)	23.1 (7.15)	3.0 (0.48)	3.8 (0.53)	0.0001*	0.0305	0.9957	0.9196	0.0001
Distance-to-edge (m)	1.0 (0.06)	9.9 (1.67)	1.1 (0.07)	10.7 (2.33)	13.9 (3.00)	0.0001*	0.9967	0.7483	0.2563	0.0001
Stem density (stems m^{-2})	394 (86.0)		585 (93.0)			0.1423				
SAV coverage (%)		66.1 (7.39)		18.1 (6.02)		0.0000*				

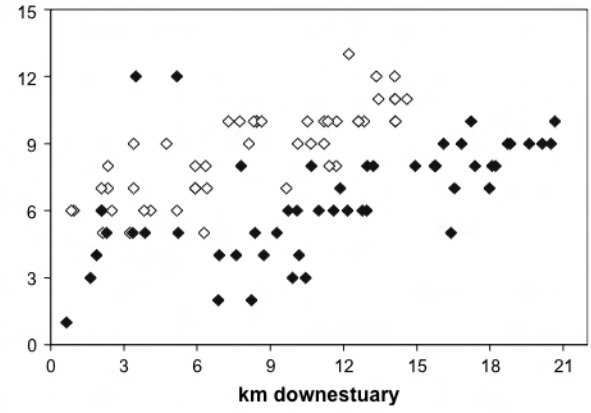

Fig. 2. Plot of salinity vs distance down-estuary (km from the upstream end of transects) in inflow and reference areas. Filled and open symbols represent samples from inflow and reference areas, respectively.

Among decapod crustaceans, brown shrimp ranked third in abundance and second in biomass. Brown shrimp in our samples were 10–87 mm TL (mean = 47.6 mm ± 1.84 SE) in size. Other abundant decapod crustacean species in our samples included Harris mud crab *Rhithropanopeus harrisii*, riverine grass shrimp *Palaemonetes paludosus*, heavy mud crab *Sesarma reticulatum*, brackish grass shrimp *Palaemonetes intermedius*, and blue crab *Callinectes sapidus*. These species, together with brown shrimp, accounted for 81% of the crustaceans taken in our study.

Four abundant species accounted for 94% of the total fishes in our samples. Rainwater killifish *Lucania parva* was the most abundant (80% of total). The other three commonly collected fishes included gulf pipefish *Syngnathus scovelli*, sheepshead minnow *Cyprinodon variegatus*, and naked goby *Gobiosoma bosc*.

Mean densities of most decapod crustaceans were highest in one of the four vegetated habitat types we sampled and were generally low over nonvegetated bottom (Table 2, Fig. 3). Exceptions were brown shrimp and blue crab; densities for these two species were not significantly different among habitat types (Table 2). Harris mud crab had highest densities in reference SAV, whereas densities of heavy marsh crab, brackish grass shrimp, and *Palaemonetes* spp. were highest in reference marsh. Densities of riverine grass shrimp were higher in inflow SAV than at reference non-marsh (SAV and SNB) sites. Fishes were most numerous in vegetated habitat types as well (Table 2, Fig. 3). Inflow SAV contained the highest mean densities of gulf pipefish, whereas reference marsh had the highest densities of sheepshead minnow. Mean densities of rainwater killifish were not significantly different among vegetated habitat types (Table 2).

The pattern for biomass was similar to the density pattern for most abundant species (Table 3). For example, mean brown shrimp biomass did not differ

significantly among habitat types. Biomass and density patterns differed, however, for blue crab, Harris mud crab, and rainwater killifish. Mean biomass for blue crab and rainwater killifish was greater at inflow SAV sites than at reference SAV and SNB sites (Table 3). Mean Harris mud crab biomass was not significantly different among habitat types. Reference marsh sites contributed most gulf fiddler crab biomass and inflow SAV accounted for most clown goby biomass.

Salinity ranged from 1 to 12 at inflow sample sites and from 5 to 13 at reference sites. The relationship between salinity and abundance of brown shrimp was relatively weak. Simple regression analyses in which we regressed brown shrimp density in a sample against salinity overall and in either the inflow area or reference area were not statistically significant ($p > 0.2081$). Thus, in the first step of the ANCOVA procedure, we could not reject the null hypothesis that the slope of the interaction term (salinity × habitat type) was equal to zero ($p = 0.2368$). Because brown shrimp densities were not dependent on salinity values in the model, we could not proceed further with the ANCOVA analysis. Scatter plots showed little evidence of nonlinear relationships. If we classified the samples into salinity classes, however, we detected a significant positive relationship between mean brown shrimp density and salinity class in the reference area ($Y = 0.1351X - 0.6525$; $p = 0.0235$); 54% of the variability in mean brown shrimp abundance (ln transformed) was explained by salinity. There was no significant relationship between these variables in the inflow area.

We compared mean size among habitat types for two important fishery species. Brown shrimp were similar in size among the habitat types we sampled (ANOVA: d.f. = 4,33, $F = 0.228$, $p = 0.9206$), and size distributions of brown shrimp were similar between the inflow and reference areas. The mean size of blue crab differed among habitat types (ANOVA: d.f. = 4,38, $F = 4.238$, $p = 0.0062$). Blue crabs were significantly larger at marsh sites than in SAV (36.3 vs 21.6 mm CW; ANOVA contrast: d.f. = 1,38, $F = 13.948$, $p = 0.0006$), but a difference in blue crab size between inflow and reference areas was not detected in our analysis.

5.3. Canonical correspondence analyses

Forward selection of the environmental variables in the complete model showed that all variables, with the exception of distance-to-edge, were statistically significant at an alpha level of 0.05. In addition to distance-to-edge, SAV cover, water temperature, and dissolved oxygen were excluded from the reference model, and salinity, SAV cover, and dissolved oxygen were excluded from the inflow model. The species–environment correlations were highest for the reference area model, followed by the complete model and the inflow area model. The cumulative variation explained with the first/second axes in the analyses was 45%/70%, 57%/86%, and 38%/73% for the complete, reference area and inflow area models, respectively.

In the complete model, axis 1 was influenced most positively by marsh and stem density and most negatively by water depth (Table 4, Fig. 4a). The inflow area, SAV cover, and water temperature had negative scores on axis 2 in the model, whereas the reference area and salinity had positive scores (Table 4, Fig. 4a). Turbidity also had a relatively strong influence on both axes. Axis 1 represents a marsh (shallow) to open-water (deep) gradient; axis 2 contrasts the reference and inflow areas (Fig. 4a). The model reflected lower salinity and turbidity and higher temperature, dissolved oxygen, and SAV coverage in the inflow area relative to the reference area. The analysis also showed that turbidity was highest at reference marsh sites and temperature was highest at inflow marsh sites. Species close to the origin (0, 0), such as blue crab and rainwater killifish were ubiquitous, whereas grass shrimp, heavy marsh crab, and sheepshead minnow were more common at marsh sites than open-water sites (Fig. 4a). Brown shrimp, naked goby, and heavy marsh crab were associated with higher salinity sites. The Harris mud crab was encountered most frequently at open-water sample sites.

The reduced models for reference and inflow areas relied on smaller sets of environmental variables. Overall, the environmental-species relationships in the reference area model were similar to the complete model, although in the reference area model, the variables turbidity, dissolved oxygen, and SAV cover were not significant (Fig. 4b). In both the reference area and complete models, many species were closely tied to specific habitat characteristics. In the inflow area model, the most important variables influencing axis 1 were turbidity and marsh with positive loadings and water temperature and depth with negative loadings (Table 4). Stem density and marsh were negatively related to water depth in axis 2; water temperature was unrelated to these variables. The CCA analyses showed that the inflow area differed substantially from the reference area in terms of environmental-species relationships. In the inflow model, the plots for most species fell near the origin (Fig. 4c), indicating that these species did not respond strongly to environmental gradients. Heavy marsh crab and sheepshead minnow, however, were exceptions to this pattern because these species were associated with turbid marsh sites (Fig. 4c). The heavy marsh crab was found at sites with cooler temperatures than sheepshead minnow.

5.4. Isotope analysis

We plotted stable isotope values against distance along the transects. The inflow area was clearly influenced by the diversion, as $\delta^{15}N$ values were

Table 2
Comparison of densities (mean $m^{-2} \pm 1$ S.E.) of decapod crustaceans and fishes collected among habitat types (inflow marsh, reference marsh, inflow SAV = submerged aquatic vegetation, reference SAV, and reference SNB = subtidal nonvegetated bottom) in May. Each mean is estimated from *n* samples shown in parentheses below each habitat type. The total number of identified species collected in each taxonomic category is also given. Results (*p* values) are given for ANOVA analyses we used to compare mean densities among habitat types and a priori contrasts testing for significant differences between: 1 = marsh in the inflow area and marsh in the reference area, 2 = SAV in the inflow area and SAV in the reference area, 3 = SAV in the inflow area and SAV + SNB in the reference area, and 4 = marsh in the two areas and SAV in the two areas. An asterisk (*) indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989)

Species	Inflow area		Reference area			Total	ANOVA	Contrast *p* values			
	Marsh edge ($n = 16$)	SAV ($n = 34$)	Marsh edge ($n = 16$)	SAV ($n = 20$)	SNB ($n = 14$)		Habitat effect	(1) I Marsh vs R Marsh	(2) I SAV vs R SAV	(3) I SAV vs R SAV + R SNB	(4) I Marsh + R Marsh vs I SAV + R SAV
	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)		*p* value				
Crustaceans (total = 10 species)											
Harris mud crab	0.3 (0.25)	5.5 (1.68)	0.3 (0.12)	20.5 (5.59)	7.5 (3.21)	712	0.0001*	0.8575	0.0057	0.0938	0.0001
Riverine grass shrimp	5.4 (2.04)	3.6 (1.73)	1.6 (0.88)	1.0 (0.95)	0.0 (0.00)	252	0.0169	0.0856	0.0972	0.0261	0.0636
Palaemonetes spp.	2.6 (1.03)	1.6 (0.57)	6.8 (2.13)	1.8 (0.57)	0.1 (0.07)	240	0.0009*	0.0287	0.4261	0.5517	0.0159
Brown shrimp	0.9 (0.58)	1.4 (0.46)	0.8 (0.44)	1.1 (0.36)	0.7 (0.22)	105	0.7635				
Heavy marsh crab	0.5 (0.38)	0.0 (0.00)	4.8 (2.80)	0.0 (0.00)	0.0 (0.00)	84	0.0001*	0.0026			0.0001
Brackish grass shrimp	0.6 (0.32)	0.6 (0.35)	2.1 (0.99)	1.0 (0.68)	0.0 (0.00)	82	0.0475	0.0783	0.8858	0.5443	0.0653
Blue crab	0.9 (0.20)	1.2 (0.26)	0.5 (0.20)	0.7 (0.20)	0.4 (0.25)	80	0.0852				
Daggerblade grass shrimp	0.7 (0.44)	0.2 (0.13)	1.3 (0.52)	0.4 (0.35)	0.0 (0.00)	46					
Gulf marsh fiddler crab	0.4 (0.38)	0.0 (0.00)	0.4 (0.22)	0.0 (0.00)	0.0 (0.00)	14					
Pink shrimp	0.1 (0.06)	0.1 (0.05)	0.0 (0.00)	0.1 (0.07)	0.0 (0.00)	6					
Unidentified crayfish	0.3 (0.25)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	5					
Unidentified Xanthidae	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1 (0.07)	1					
Total crustaceans	12.6 (3.22)	14.1 (2.64)	18.6 (4.63)	26.3 (5.82)	8.7 (3.34)	1627	0.2036				
Fishes (total = 23 species)											
Rainwater killifish	6.1 (2.18)	25.9 (8.22)	8.8 (3.33)	61.7 (22.86)	1.5 (0.80)	2374	0.0251	0.7014	0.4266	0.1983	0.0537
Gulf pipefish	0.3 (0.25)	4.8 (1.03)	0.2 (0.10)	1.5 (0.68)	0.2 (0.16)	203	0.0001*	0.9591	0.0030	0.0001	0.0001
Sheepshead minnow	1.2 (0.61)	0.2 (0.10)	6.1 (2.42)	0.7 (0.30)	0.0 (0.00)	136	0.0002*	0.0105	0.3093	0.7716	0.0012
Naked goby	0.5 (0.32)	0.6 (0.18)	0.4 (0.24)	1.0 (0.39)	1.0 (0.59)	70	0.8090				
Code goby	0.0 (0.00)	0.3 (0.19)	0.0 (0.00)	1.0 (0.45)	0.3 (0.29)	32					
Inland silverside	0.0 (0.00)	0.7 (0.68)	0.0 (0.00)	0.3 (0.14)	0.0 (0.00)	29					
Unidentified fish	0.2 (0.14)	0.3 (0.19)	0.0 (0.00)	0.5 (0.40)	0.1 (0.07)	23					
Clown goby	0.0 (0.00)	0.4 (0.12)	0.0 (0.00)	0.2 (0.14)	0.1 (0.10)	21					
Unidentified Engraulidae	0.0 (0.00)	0.1 (0.06)	0.1 (0.06)	0.5 (0.22)	0.1 (0.07)	14					
Spot	0.0 (0.00)	0.1 (0.07)	0.0 (0.00)	0.1 (0.05)	0.2 (0.16)	8					
Gulf killifish	0.0 (0.00)	0.0 (0.00)	0.4 (0.44)	0.0 (0.00)	0.0 (0.00)	7					
Unidentified gar	0.2 (0.14)	0.1 (0.07)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	7					
Speckled worm eel	0.0 (0.00)	0.1 (0.04)	0.0 (0.00)	0.2 (0.11)	0.1 (0.07)	6					
Diamond killifish	0.1 (0.06)	0.0 (0.00)	0.3 (0.17)	0.0 (0.00)	0.0 (0.00)	5					
Bay anchovy	0.0 (0.00)	0.1 (0.09)	0.0 (0.00)	0.1 (0.07)	0.0 (0.00)	5					
Bayou killifish	0.0 (0.00)	0.0 (0.00)	0.3 (0.14)	0.0 (0.00)	0.0 (0.00)	4					
Unidentified Gobiidae	0.1 (0.06)	0.1 (0.05)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	4					
Largemouth bass	0.0 (0.00)	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	4					
Atlantic croaker	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1 (0.07)	0.1 (0.07)	3					
Unidentified Atherinidae	0.0 (0.00)	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2					
Bay whiff	0.0 (0.00)	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2					
Spotted seatrout	0.0 (0.00)	0.1 (0.04)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2					

Pinfish	0.1 (0.06)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	2				
Unidentified Bothidae	0.0 (0.00)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Fat sleeper	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Spotted gar	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Alligator gar	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Striped mullet	0.0 (0.00)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Atlantic needlefish	0.0 (0.00)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1				
Total fishes	8.9 (2.36)	34.1 (8.69)	16.6 (3.92)	67.6 (22.99)	3.6 (1.24)	2969	0.0013*	0.3799	0.5785	0.0382	0.0268

significantly higher ($p < 0.0001$) for animals collected in the inflow area than for those taken in the reference area (Table 5, Fig. 5). This result is consistent with many riverine systems that have water masses enriched in $\delta^{15}N$ (Cabana and Rasmussen, 1996; Hebert and Wassenaar, 2001), which has also been documented for the lower Mississippi River (Kendall et al., 2001; Wissel and Fry, 2005). Average adjusted $\delta^{15}N$ values (‰) for shrimp were 11.1 ± 0.1 SE and 8.8 ± 0.2 SE from the inflow and reference areas, respectively. For this spatial comparison, measured brown shrimp values were adjusted by adding 1.43‰ so that mean $\delta^{15}N$ values for brown shrimp and grass shrimp were equivalent.

The two areas had similar $\delta^{13}C$, with values increasing from low-salinity sample sites near the diversion to higher salinity sites nearer the coast. Additionally, we detected significant differences between habitat types ($p = 0.005$) with marsh samples having higher $\delta^{13}C$ values than open-water sites (Table 5).

We also observed significant differences between brown shrimp and grass shrimp (Table 5). Grass shrimp were enriched (relative to brown shrimp) by 1.1‰ for carbon isotopes ($p = 0.006$) and 1.4‰ for nitrogen isotopes ($p = 0.001$).

Based on our results, the $\delta^{34}S$ values were not significantly different between areas, habitats, and species, except for one significant location by species interaction. Brown shrimp had significantly higher $\delta^{34}S$ values ($p = 0.03$) in the inflow area compared to the reference area (Table 5, Fig. 6).

6. Discussion

We found clear evidence that freshwater inflows from the Caernarvon structure in 2001 affected water quality, habitat, and macrofaunal distributions during May in the Breton Sound estuary. Diverted river water reduced salinities in the upper inflow area, and likely influenced the salinity pattern we observed during our study. Many sites ($n = 18$) in the inflow area had salinities ≤ 5, and we collected several freshwater taxa (e.g., crayfish, gars, and largemouth bass) exclusively in this area. The riverine grass shrimp, a freshwater caridean shrimp, also was much more abundant in the inflow area than the reference area. Only three reference sample sites had salinities ≤ 5, and more reference sites than inflow sites had salinities that exceeded 10 (7 vs 2). Salinities in the reference area at the time of our study were characteristic of conditions typical for this time of year in the area prior to construction of the Caernarvon structure (Orlando et al., 1993), an indication that freshwater introduced into the estuary by the structure had little influence on salinities north of Bayou Terre Aux Boeufs.

These freshwater flows also expanded the habitat area for macrofauna by increasing SAV coverage in the

Table 3
Comparison of biomasses (mean ± 1 S.E.) in grams of decapod crustaceans and fishes collected among habitat types (inflow marsh, reference marsh, inflow SAV = submerged aquatic vegetation, reference SAV, and reference SNB = subtidal nonvegetated bottom) in May. Each mean is estimated from *n* samples shown in parentheses below each habitat type. Results (*p* values) are given for ANOVA analyses we used to compare mean biomass among habitat types and a priori contrasts testing for significant differences between: 1 = marsh in the inflow area and marsh in the reference area, 2 = SAV in the inflow area and SAV in the reference area, 3 = SAV in the inflow area and SAV plus SNB in the reference area, and 4 = marsh in the two areas and SAV in the two areas. An asterisk (*) indicates that the ANOVA probability value was significant at the 5% level after alpha was adjusted as described by Rice (1989)

Species	Inflow area		Reference area			Total	ANOVA	Contrast *p* values			
	Marsh edge ($n = 16$)	SAV ($n = 34$)	Marsh edge ($n = 16$)	SAV ($n = 20$)	SNB ($n = 14$)		Habitat effect	(1) I Marsh vs R Marsh	(2) I SAV vs R SAV	(3) I SAV vs R SAV + R SNB	(4) I Marsh + R Marsh vs I SAV + R SAV
	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)	Mean (S.E.)		*p* value				
Crustaceans											
Blue crab	4.6 (2.19)	3.5 (1.52)	2.5 (1.34)	0.0 (0.03)	0.5 (0.27)	243.8	0.0252	0.1619	0.0409	0.0118	0.1205
Brown shrimp	0.6 (0.45)	1.4 (0.48)	0.7 (0.34)	3.0 (1.67)	0.6 (0.20)	114.8	0.6716				
Harris mud crab	0.0 (0.00)	1.3 (0.31)	0.1 (0.09)	0.4 (0.16)	1.3 (0.35)	79.1	0.0002*	0.7105	0.8674	0.3449	0.0001
Heavy marsh crab	0.4 (0.29)	0.0 (0.00)	4.0 (1.75)	0.0 (0.00)	0.0 (0.00)	70.3	0.0001*	0.0002			0.0001
Riverine grass shrimp	1.0 (0.45)	0.7 (0.33)	0.3 (0.15)	0.0 (0.00)	0.0 (0.03)	43.0	0.0360	0.1125	0.0711	0.0283	0.1040
Gulf marsh fiddler crab	0.3 (0.27)	0.0 (0.00)	2.3 (1.53)	0.0 (0.00)	0.0 (0.00)	41.3	0.0150	0.0482			0.0054
Palaemonetes spp.	0.7 (0.37)	0.2 (0.09)	0.8 (0.29)	0.1 (0.06)	0.0 (0.04)	33.8	0.0042*	0.4336	0.5293	0.2530	0.0010
Brackish grass shrimp	0.1 (0.05)	0.1 (0.07)	0.3 (0.15)	0.1 (0.08)	0.0 (0.02)	12.4					
Daggerblade grass shrimp	0.1 (0.09)	0.0 (0.03)	0.1 (0.08)	0.0 (0.00)	0.0 (0.00)	4.9					
Unidentified Xanthidae	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.01)	0.2					
Unidentified crayfish	0.0 (0.01)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1					
Pink shrimp	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1					
Total crustaceans	7.8 (2.10)	7.2 (1.69)	11.1 (2.83)	3.6 (1.87)	2.5 (0.42)	1627.0	0.0238	0.9841	0.2206	0.0241	0.0641
Fishes											
Rainwater killifish	0.4 (0.18)	1.3 (0.27)	0.3 (0.11)	0.7 (0.31)	0.5 (0.21)	74.7	0.0082	0.7470	0.2815	0.0082	0.0104
Spot	0.0 (0.00)	0.9 (0.72)	0.0 (0.00)	0.9 (0.94)	1.1 (0.78)	65.6	0.3842				
Striped mullet	0.0 (0.00)	1.7 (1.70)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	57.9	0.7540				
Gulf pipefish	0.0 (0.05)	0.5 (0.10)	0.0 (0.01)	0.2 (0.12)	0.0 (0.02)	19.8	0.0001*	0.8229	0.0019	0.0001	0.0009
Clown goby	0.0 (0.00)	0.4 (0.15)	0.0 (0.00)	0.2 (0.19)	0.0 (0.00)	16.8	0.0021*		0.0102	0.0009	0.0111
Naked goby	0.2 (0.13)	0.2 (0.05)	0.1 (0.08)	0.0 (0.02)	0.2 (0.08)	15.0	0.9397				
Inland silverside	0.0 (0.00)	0.3 (0.24)	0.0 (0.00)	0.1 (0.11)	0.1 (0.10)	13.5	0.4185				
Sheepshead minnow	0.1 (0.06)	0.0 (0.00)	0.7 (0.33)	0.0 (0.00)	0.0 (0.00)	12.1	0.0003*	0.0030	0.9846	0.9868	0.0006
Atlantic croaker	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.7 (0.73)	0.1 (0.11)	10.5					
Pinfish	0.2 (0.25)	0.1 (0.08)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	6.7					
Speckled worm eel	0.0 (0.00)	0.1 (0.07)	0.0 (0.00)	0.1 (0.10)	0.0 (0.01)	4.3					
Diamond killifish	0.0 (0.03)	0.0 (0.00)	0.1 (0.09)	0.0 (0.00)	0.0 (0.00)	2.5					
Bay anchovy	0.0 (0.00)	0.0 (0.04)	0.0 (0.00)	0.1 (0.06)	0.0 (0.01)	2.3					
Gulf killifish	0.0 (0.00)	0.0 (0.00)	0.1 (0.09)	0.0 (0.00)	0.0 (0.00)	1.5					
Unidentified fish	0.0 (0.02)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.5					
Bay whiff	0.0 (0.00)	0.0 (0.04)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.4					
Bayou killifish	0.0 (0.00)	0.0 (0.00)	0.1 (0.07)	0.0 (0.00)	0.0 (0.00)	1.4					
Code goby	0.0 (0.00)	0.0 (0.02)	0.0 (0.00)	0.0 (0.01)	0.0 (0.00)	1.1					
Largemouth bass	0.0 (0.00)	0.0 (0.02)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.1					
Unidentified Bothidae	0.0 (0.00)	0.0 (0.03)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.9					
Unidentified Atherinidae	0.0 (0.00)	0.0 (0.02)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.7					
Spotted seatrout	0.0 (0.00)	0.0 (0.01)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5					
Fat sleeper	0.0 (0.01)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1					

Unidentified Engraulidae	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1					
Alligator gar	0.1 (0.06)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.1					
Unidentified gar	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0					
Unidentified Gobiidae	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0					
Spotted gar	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0					
Atlantic needlefish	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0					
Total fishes	1.1 (0.36)	5.6 (1.84)	1.4 (0.48)	3.1 (1.33)	2.1 (1.00)	312.1	0.0017*	0.7045	0.0643	0.0013	0.0054

inflow area. SAV, as well as marsh edge habitat, generally supported higher mean densities of total fishes and total decapod crustaceans than nearby nonvegetated sites. Mean densities of fishes were 9.5, 18.8, 2.5, and 4.6 times higher, and densities of crustaceans were 1.6, 3.0, 1.4, and 2.1 times higher in inflow SAV, reference SAV, inflow marsh, and reference marsh, respectively, than densities over nonvegetated bottom. This pattern of higher nekton densities in vegetated than nonvegetated areas is consistent with interhabitat comparison studies conducted in other shallow estuarine systems (Zimmerman and Minello, 1984; Heck et al., 1989; Lubbers et al., 1990; Thomas et al., 1990; Rozas and Minello, 1998; Castellanos and Rozas, 2001). Within vegetated areas, most abundant species were associated with specific habitat types. For example, heavy marsh crab and sheepshead minnow were most abundant in the reference area and found exclusively at marsh sites. Gulf pipefish were most closely associated with SAV in the inflow area. Only two species, brown shrimp and rainwater killifish, were important constituents of all five habitat types included in our study.

Overall, we observed what appeared to be a much stronger response to environmental gradients by taxa in the reference area than the inflow area. The most likely cause of this homogenization of the nekton community in the inflow area was a change in the distribution of habitat types, specifically increased aquatic vegetation. Based on our samples, all of the shallow portions of the inflow area contained submerged vegetation (rooted vascular plants or macroalgae), whereas $>40\%$ of substrate of shallow areas in the reference area did not support aquatic vegetation. Despite the presence of salinity gradients along both transects, salinity did not appear to affect community composition in the inflow area, even though salinity was an important environmental predictor in the reference area. The changes in community structure we documented between the two areas mostly involved changes in density rather than shifts in species composition, but these changes are consistent with larger changes associated with disturbed aquatic systems (Capriulo et al., 2002; Young and Potter, 2003; Worms and Duffy, 2003). The observed phenomenon of homogenization may warrant further attention in studies related to the impacts of diversions on downstream coastal systems. Although some increase in aquatic vegetation may be beneficial and provide more fisheries habitat, excessive development of SAV beds documented in the nearby Atchafalaya Basin (which receives higher inputs of this same Mississippi River basin water) can have a negative impact on aquatic organisms (Engel, 2003; Colón-Gaud, 2003).

Previous work suggested that nutrients delivered with the diverted river water were readily taken up by estuarine biota (Lane et al., 2004). Accordingly, shrimp in the inflow area were enriched in ^{15}N, reflecting the

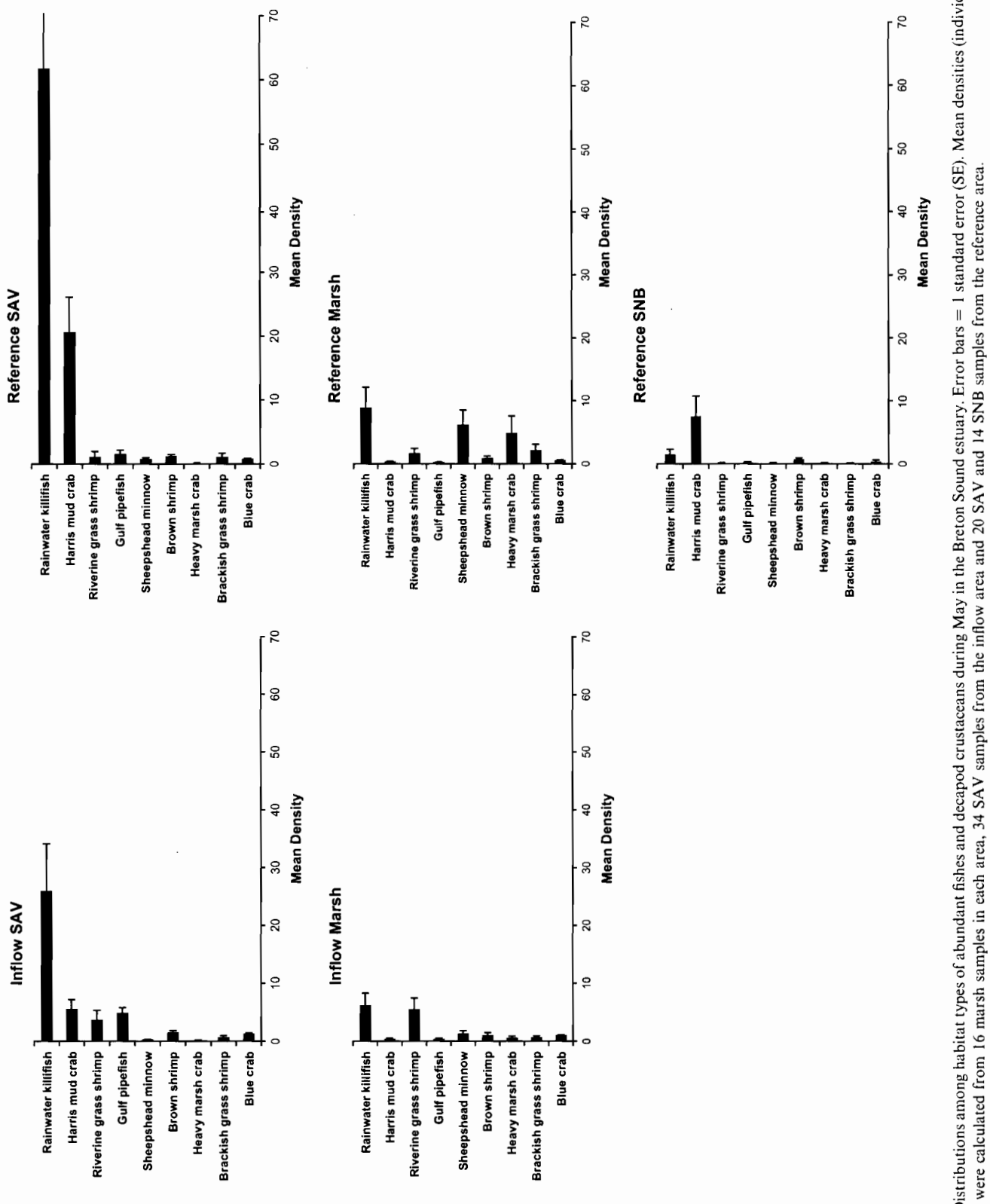

Fig. 3. Distributions among habitat types of abundant fishes and decapod crustaceans during May in the Breton Sound estuary. Error bars = 1 standard error (SE). Mean densities (individuals m^{-2}) and SEs were calculated from 16 marsh samples in each area, 34 SAV samples from the inflow area and 20 SAV and 14 SNB samples from the reference area.

Table 4
Weighted correlation matrix for the canonical correspondence analyses of the complete, reference, and inflow area models. SA = species axis, EA = environmental axis

Variable	Complete				Reference				Inflow			
Axis	SA1	SA2	EA1	EA2	SA1	SA2	EA1	EA2	SA1	SA2	EA1	EA2
Inflow	−0.04	−0.23	−0.05	−0.35	–	–	–	–	–	–	–	–
Marsh	0.74	0.11	0.89	0.16	0.84	0.05	0.97	0.08	0.37	0.49	0.45	0.65
Water depth	−0.75	−0.04	−0.90	−0.06	−0.84	0.09	−0.97	0.14	−0.35	−0.53	−0.42	−0.70
Stem density	0.56	−0.08	0.67	−0.12	0.60	−0.12	0.69	−0.18	−0.02	0.61	−0.02	0.81
Water temperature	0.21	−0.29	0.25	−0.45	0.33	−0.12	0.38	−0.18	−0.39	0.26	−0.47	0.34
Turbidity	0.43	0.37	0.51	0.58	–	–	–	–	0.50	0.36	0.60	0.48
Salinity	0.06	0.40	0.07	0.62	−0.02	0.46	−0.03	0.74	–	–	–	–
SAV cover	−0.09	−0.31	−0.11	−0.49	–	–	–	–	–	–	–	–
Dissolved oxygen	−0.09	−0.24	−0.11	−0.37	–	–	–	–	–	–	–	–

high $\delta^{15}N$ values of Mississippi River inputs, especially nitrate (Fry and Allen, 2003) and particulate organic nitrogen (PON); these nitrogen species have average values in the 7–8‰ range and are generally higher in river water than in coastal waters lacking riverine inputs (Fry and Allen, 2003; Wissel et al., in press). Lack of high $\delta^{15}N$ values in the area north of Bayou Terre Aux Boeufs is consistent with its use as a reference area (i.e., it was relatively free of river input).

Shrimp $\delta^{13}C$ values reflected the estuarine salinity gradient, increasing down-estuary as predicted from simple salinity-based mixing models (Fry, 2002a). The higher $\delta^{13}C$ values observed in our study for marsh-collected shrimp are often seen in marshes where attached benthic microalgae are an important food source (Currin et al., 1995).

The isotopic values for shrimp also differed by species. Although all three species in our analysis are omnivorous, brown shrimp consume relatively more animal material than grass shrimp (McTigue and Zimmerman, 1998; Fleeger et al., 1999; Zimmerman et al., 2000). Because of their tendency toward carnivory, brown shrimp would be expected to have higher $\delta^{13}C$ and $\delta^{15}N$ values than grass shrimp; higher $\delta^{13}C$ and $\delta^{15}N$ values have been associated with higher trophic levels (Fry et al., 2003). However, we observed the opposite pattern along both transects, which could be misinterpreted as evidence for brown shrimp feeding at a lower trophic level than grass shrimp. A similar offset by 1–2‰ between grass shrimp and other organisms such as brown shrimp, barnacles, and bay anchovies has been observed in several Louisiana estuaries (Wissel and Fry, unpublished data), and rather may be related to habitat preference than to trophic position. Epiphytes, as the preferred food of grass shrimp (Fleeger et al., 1999), are located in a narrow boundary layer where nutrient supply may be limiting. A limited supply of dissolved inorganic carbon for photosynthesis generally reduces fractionation (O'Leary, 1988; Fogel et al., 1992) and results in enriched $\delta^{13}C$ values. Similarly, the nitrogen dynamics also are different in the boundary layer. A possible explanation for the elevated $\delta^{15}N$ values found in grass shrimp could be that recycled ammonium with high $\delta^{15}N$ values is an important nutrient for epiphytes at the boundary layer, and these elevated values are passed from epiphytic algae up the food web.

Evidence for an effect on brown shrimp distributions in the estuary caused by freshwater inflows from the Caernarvon structure was inconclusive. Brown shrimp densities in the estuary were relatively low, but densities did not differ significantly among the habitat types we sampled. Moreover, brown shrimp densities in habitat types within the inflow area were at least as high as densities in the same habitat types within the reference area, an area that receives little, if any, freshwater from the structure. Although densities of brown shrimp were low in both the inflow and reference areas, these densities were comparable to those documented in other studies of similar habitat types and low-salinity (<10) areas of Louisiana. In the Terrebonne Bay estuary, Rozas and Reed (1993) reported mean brown shrimp densities during April and May of 0.8 m^{-2} and 2.3 m^{-2} in high *Distichlis spicata* marsh and low *Spartina alterniflora* marsh, respectively. Comparable densities (2.0 m^{-2}) of brown shrimp were observed in a recent study of shallow ponds in the same general area (Baltz et al., personal communication). In the Barataria estuary, Rozas and Minello (1999) reported brown shrimp mean densities during May of 0.4 m^{-2} and 1.3 m^{-2} in *Spartina patens* marsh and SAV, respectively.

Salinity at sample sites ranged between 1 and 13, and we expected to see a corresponding gradient in brown shrimp density if salinity had a strong influence on the distribution of this species. However, regression analyses indicated no such pattern in the inflow area. In the reference area, where salinities were higher, there was a relationship between salinity (as a class variable) and mean density of brown shrimp. The CCA analysis also showed a significant correlation between brown shrimp abundance in the reference area and increasing salinity.

The issue of how brown shrimp respond to salinity patterns in estuaries is still a matter of debate. Barrett and

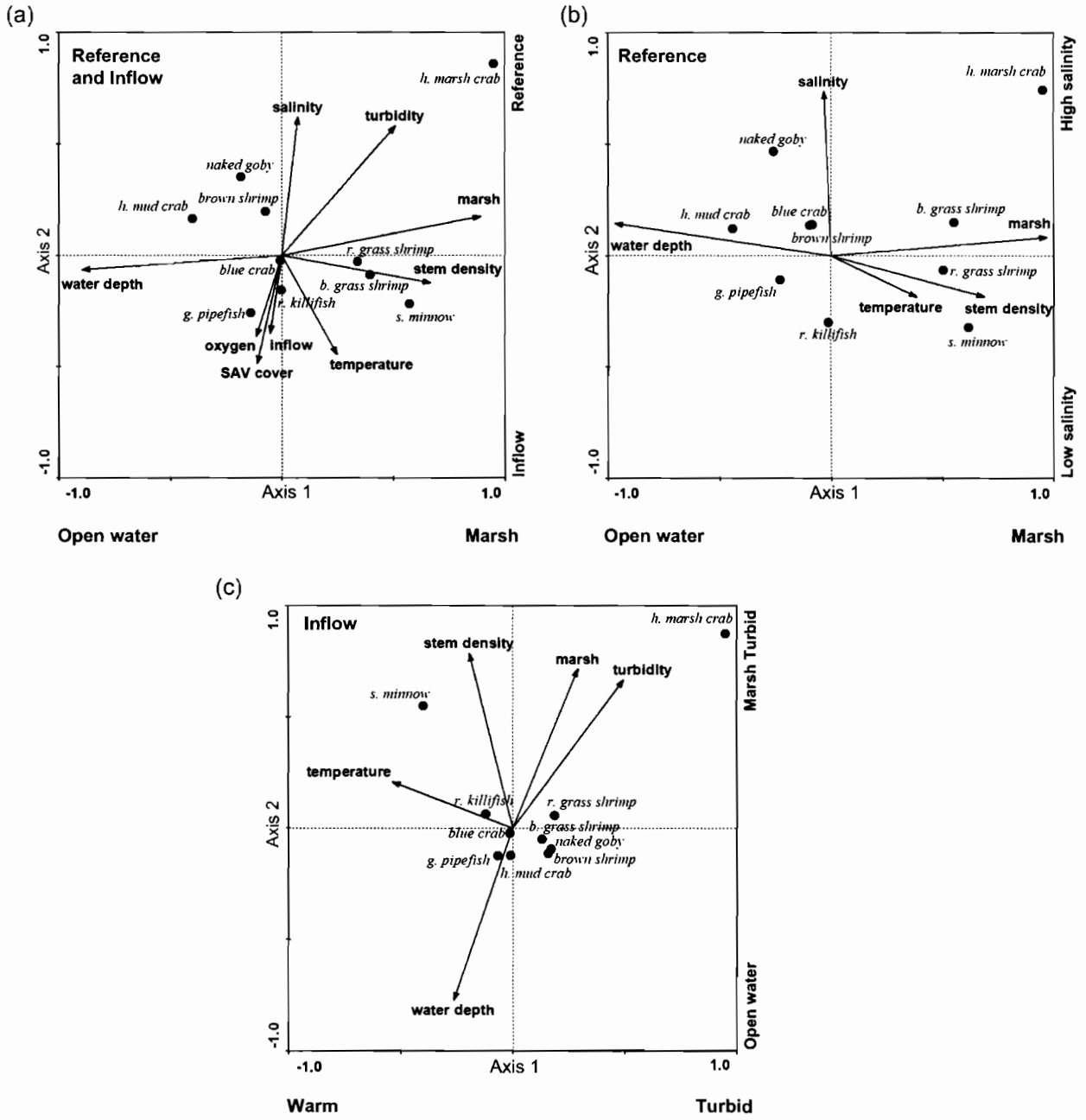

Fig. 4. Association of taxa and environmental variables based on canonical correspondence analyses for (a) the complete data set (inflow and reference areas combined), (b) the reference area, and (c) the inflow area. Black dots represent the centroids for each taxon. The length of arrows represents the relative importance of environmental variables in associations. Arrows pointing in the same direction indicate that the variables are positively correlated, whereas arrows pointing in the opposite direction indicate a negative correlation. Arrows that are perpendicular indicate that the variables are not correlated. h. marsh crab = heavy marsh crab, h. mud crab = Harris mud crab, r. grass shrimp = riverine grass shrimp, b. grass shrimp = brackish grass shrimp, r. killifish = rainwater killifish, g. pipefish = gulf pipefish, and s. minnow = sheepshead minnow.

Gillespie (1973), Longley (1994), and Minello (1999) have all postulated that salinity affects brown shrimp abundance and distributions in estuarine environments, and concluded that brown shrimp are most abundant at salinities >15–19. Gunter et al. (1964) reported that brown shrimp were most abundant at salinities >10. Zimmerman et al. (1990a) found brown shrimp densities in Galveston Bay to be highest at mid-bay and lower-bay stations where salinities were moderate to high. Densities of brown shrimp in Lavaca Bay, TX decreased following floods on the Lavaca River (Zimmerman et al., 1990b). In contrast, Thomas (1999) analyzed 6 yr of trawl data from the Louisiana Department of Wildlife and Fisheries' (LDWF) Fisheries-Independent Monitoring Program and found that the highest catch of brown shrimp occurred at sites with salinities <10. Parker (1970)

Table 5
Results of the ANOVAs comparing the effects of location (reference, inflow areas), habitat (marsh, water = SAV plus SNB), and species (*Palaemonetes* = *P. paludosus* plus *P. intermedius*, *F. aztecus* = *Farfantepenaeus aztecus*) on carbon, nitrogen, and sulfur isotopic values. Means (and 1 standard error) of isotopic values, degrees of freedom (d.f.), *F* values, and *p*-values are presented for each main effect and interaction that had a *p*-value < 0.05. Tukey adjustments were used for all pairwise comparisons

Element	Factor	d.f.	*F* value	Level A		Level B		*p* value
^{13}C	Habitat	1	8.15	Marsh = −18.2	(0.2)	Water = −19.7	(0.2)	0.005
	Species	1	8.28	*Palaemonetes* = −18.8	(0.2)	*F. aztecus* = −19.9	(0.2)	0.006
^{15}N	Location	1	49.39	Reference = 8.8	(0.2)	Inflow = 11.1	(0.1)	0.0001
	Species	1	2.72	*Palaemonetes* = 10.9	(0.2)	*F. aztecus* = 9.5	(0.2)	0.001
^{34}S	Location × species	1	0.05	*F. aztecus* × Inflow = 9.3	(0.3)	*F. aztecus* × Reference = 6.5	(0.4)	0.03

sampled brown shrimp in Galveston Bay and reported that shrimp were concentrated in shallow water along marsh shorelines where salinities were <5–10.

Salinities in our study area were all <15, and we cannot address questions about brown shrimp distribution over a larger salinity range. However, overall densities of brown shrimp in our study area were relatively low in relation to densities observed in higher salinity regions of Texas and Louisiana (Minello, 1999; Rozas and Minello, 2001). We did observe other evidence consistent with a negative response of brown shrimp to freshwater inflows from the river diversion. We collected no brown shrimp from the first 7 km of the inflow area transect where salinities were ≤5. Although present in these low-salinity waters near the upper end of the transect (unpublished LDWF trawl data), brown shrimp clearly were more abundant farther down the estuary.

The stable isotope analysis for sulfur also provided evidence for a negative response by brown shrimp to freshwater inflows. Generally, sulfur isotope values in estuarine animals are positively related to salinity (Fry, 2002a). In the Mississippi River, $\delta^{34}S$ values for fish are commonly between −5 and 0‰ (Fry, 2002b), while in marine environments values increase towards the value of seawater sulfate, 21‰ (Fry, 2002b). We generally observed this predicted down-estuary trend of increasing $\delta^{34}S$ isotope values for grass shrimp, but not for brown shrimp. For brown shrimp in the inflow area, where salinities were lower than in the reference area, one would expect lower $\delta^{34}S$ values, but we observed the opposite, higher $\delta^{34}S$ values relative to the reference area. One possible explanation for this pattern is that brown shrimp are more mobile than grass shrimp, and had been recently displaced down-estuary where they acquired higher $\delta^{34}S$ values during feeding and growth. The brown shrimp we collected thus may have been moving back up the estuary after having been displaced earlier in the year by freshwater inflows from the diversion. Although speculative, this explanation does reconcile the observed low salinities in the inflow area with high $\delta^{34}S$ values measured in brown shrimp. An alternative explanation for these sulfur stable isotope results is that salinities

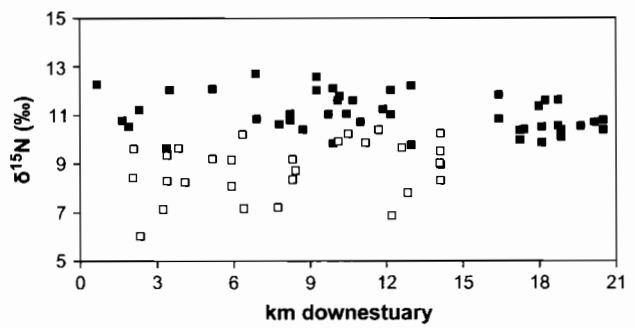

Fig. 5. Plot of $\delta^{15}N$ values (‰) of shrimp vs distance down-estuary (km from the upstream end of transects) in inflow and reference areas. Brown shrimp values have been adjusted upwards by 1.43‰, and grass shrimp values are measured values. Filled and open symbols represent samples from inflow and reference areas, respectively.

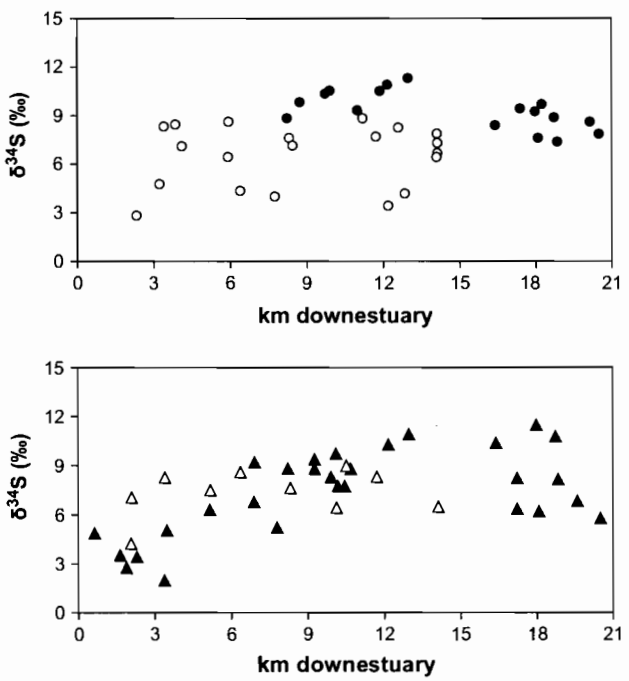

Fig. 6. $\delta^{34}S$ (‰) values for brown shrimp (*Farfantepenaeus aztecus*; upper panel) and grass shrimp (*Palaemonetes paludosus* and *Palaemonetes intermedius*; lower panel) vs distance down-estuary (km from the upper end of the transect). Filled and open symbols represent samples from inflow and reference areas, respectively.

were higher in the inflow area than the reference area during the two-week period prior to our sampling trip. However, continuous salinity recorders in the inflow area on Crooked Bayou (~5 km northeast of our transect) and False River (~2 km northeast of our transect) showed that mean salinities over this two-week period were actually lower (6.0 vs 7.3–7.5) than during the week when we collected our samples (Louisiana Department of Natural Resources, LDNR). Salinity recorded in the reference area at Hopedale Lagoon changed little (means: 2-wk prior = 10.5; sampling week = 10.8) over this same three-week period (LDNR).

The uncertainty surrounding the environmental requirements of brown shrimp is surprising, given the importance of the fishery for this species. A better understanding of these requirements for brown shrimp and other fishery species would make it possible to design and operate large freshwater diversion structures in a manner that would both restore estuarine areas and benefit coastal fisheries. A combination of controlled experiments and modeling studies may offer the best approach for elucidating the relationship between brown shrimp productivity and freshwater inflows (and changes in salinity and water temperature). Future research to examine the effects of freshwater inflows on brown shrimp production should take advantage of the potential for controlled releases from the Caernarvon structure and incorporate a good BACI design to detect short-term salinity effects on brown shrimp and other organisms (Underwood, 1992). Information from such studies along with other relevant ecological data could be used to select the most efficient operating schedule for diversion structures.

In summary, releases from the Caernarvon structure freshened the inflow area as intended and increased SAV and daytime dissolved oxygen concentrations. The response by macrofauna to these increased freshwater flows and habitat changes was more subtle. Changes in community structure involved mostly changes in density and biomass rather than shifts in species composition. Although we detected no strong effect of the freshwater diversion on brown shrimp abundance in the inflow area, our results also suggest that shrimp in the inflow area had been growing in higher salinity waters, possibly following downstream displacement by the diversion. Species that would benefit most from continued freshwater diversions are likely to be those species that both use SAV as nursery habitat and thrive in a low-salinity environment. Nutrients carried by water from the structure were incorporated into the estuarine food web, and these nutrient inputs, together with an increase in SAV habitat, may enhance overall secondary productivity in the inflow area. Close monitoring of environmental conditions in the inflow area should continue, however, for excessive development of SAV beds or a reduction in water quality.

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